

GENETICS OF THE ROSE.

MAJOR C. C. HURST: Since the War I have devoted myself to a study of the genetics of the Rose. A comprehensive collection of the known species, sub-species and hybrids has been got together in the Cambridge Botanic Garden from various sources, including wild species collected by my wife and myself in England and in five cantons of Switzerland, together with plants raised from seeds sent to me by correspondents and travellers in North America, Mexico, Turkestan, Siberia, China and Japan. Amongst these I am particularly grateful to Professor T. D. A. Cockerell, of Colorado, who has been most assiduous and generous in collecting, pickling and preserving for me specimens of wild species of *Rosa* in his various expeditions to Siberia (Lake Baikal), Russian Turkestan, Manchuria, and other remote places. Professor Cockerell has also sent me living plants of the rare American Rose, *Hesperhodos minutifolia* sub-species *stellata*, which are now doing well in the Botanic Garden at Cambridge, and so far as I know are unique in Europe.

Professor R. Ruggles Gates, of King's College, London, has also been good enough to collect seeds of Wild Roses for me in Russian Lapland, north of the Arctic Circle, and also from the Mackenzie River district in Canada, south of the Arctic Circle.

Dr. Eileen Erlanson, of the Michigan Botanic Gardens, who has made a special study of North American Rose species and varieties, has generously sent me a large number of seeds and specimens collected in Michigan, as well as some interesting seeds of Roses from Alaska.

Many plants have been raised at Cambridge from the seeds of these collections, and it is already evident that this material will help to

solve the important problem of the distribution and status of the octoploid, hexaploid, tetraploid and diploid forms of the polymorphous species formerly included under the common name of *R. acicularis*.

Dr. Heslop Harrison, who has made a special study of British Roses, has from time to time kindly sent me seeds and cuttings of interesting Roses from co. Durham.

I am much indebted to the Directors of the Botanic Gardens at Kew, Oxford, Cambridge and Basel, to Colonel Gravereaux of La Roseraie de l'Hay, Paris, and to Dr. Mary Carew-Hunt (who kindly allowed me to select 80 specimens from the collection of the late Canon Carew-Hunt at Albury, Oxford) for free access to their collections in obtaining my material. I wish also to acknowledge the facilities allowed me in my work in the Botanic Garden at Cambridge by Mr. H. Gilbert-Carter (Director), Mr. F. G. Preston (Superintendent), and Mr. Reginald Cory (Benefactor), all of whom have gone out of their way to help me to secure land, labour, and valuable material. My best thanks are also due to Professor A. C. Seward and Mr. F. T. Brooks, of the Botany School, and Professor Stanley Gardiner of Cambridge, for the laboratory accommodation necessary for the preparation of cytological material, and for microscopical research.

In the examination of herbarium specimens at the British Museum and the Linnean Society of London, I am much indebted to Dr. A. B. Rendle, Miss Willmott and Mr. Baker, and also to the late Dr. Daydon Jackson, whose loss we deeply deplore. Lastly, I owe to my wife all the drawings, photographs, paintings and herbarium specimens collected during the last six years, as well as a considerable amount of assistance in genetical experiments, laboratory work and microscopical researches.

The Rose material has been analysed in three different ways in accordance with the methods of three different sciences: Taxonomy, Genetics, and Cytology.

First.—About 100 characters of each species, sub-species and variety have been examined and tabulated.

Second.—Numerous experimental crosses have been made between various species, sub-species and varieties and the results recorded and tabulated. Many known hybrids have also been analysed.

Third.—The chromosomes of 674 species, sub-species, varieties and hybrids have been examined and counted in various stages in both body-cells and germ-cells under high-powered microscopes.

The results of these combined experiments and researches have proved to be of considerable importance, and in many cases surprising, and quite unexpected results have been obtained. I fear that several large volumes will be required to record the results already secured, and so far as one can see we are yet merely on the threshold of important results to come.



FIG. 1 (a).



FIG. 1 (b).

Diploid Roses with 14 chromosomes in body-cells and seven in male and female germ-cells.

- (a) Fourteen chromosomes in body-cell of the old Pink China Rose (AA). (See pages 40 and 47.)
- (b) Fourteen chromosomes in body-cell of the Polyantha Pompon Rose "Eblouissant" (AA). (See page 41.)

The most important results have come from the counting of the chromosomes. A Rose plant, like other plants and animals, is made up of millions of minute cells, which form the various tissues. Each cell contains a round, central body known as the nucleus. Each nucleus contains a number of microscopical rod-like bodies which stain rapidly with chemical dyes, and for that reason are called chromosomes. These chromosomes carry the Mendelian factors, or *genes* as we now call them, which differentiate the various characters of the Rose. In the body-cells the chromosomes usually consist of pairs, one of which came

from the male parent and the other from the female parent. In the male and female final germ-cells (gametes) the chromosomes are single, so that a pollen-nucleus and an egg-nucleus carry usually one-half the number of chromosomes that are contained in the body-cells. When fertilisation takes place the two singles come together and make a pair of chromosomes. As an illustration of how this works in a given case, we will take two well-known Roses and cross them together. The female parent is *multiflora* from Japan, with Tall Summer-flowering stems and Single White flowers. The male parent is *chinensis* from China, with Dwarf Perpetual-flowering stems and Semi-double Pink flowers. Each parent has seven pairs of chromosomes in its body-cells and seven single chromosomes in its germ-cells. From experiments we know that the Mendelian gene for Tall Summer-flowering stems is located in one chromosome of the seven present in the egg-nucleus of *multiflora*, while the gene for Single flowers is located in a second chromosome, and the gene for White flowers is located in a third chromosome.

Similarly the gene for Dwarf Perpetual-flowering stems is located in one chromosome of the seven present in the pollen-nucleus of *chinensis*, while the gene for Double flowers is located in a second chromosome, and the gene for Pink flowers is located in a third chromosome. After fertilisation the cells of the hybrid contain seven pairs of chromosomes, seven from each parent. The chromosome carrying the gene for Tall Summer-flowering from *multiflora* pairs off with the chromosome carrying the gene for Dwarf Perpetual-flowering from *chinensis*, as do the two chromosomes carrying genes for Single and Double flowers, and the two chromosomes carrying genes for White and Pink flowers. The resulting hybrid produces Tall Summer-flowering stems with Semi-double Pink flowers, since these characters are dominant while Dwarf Perpetual-flowering stems and Single White flowers are recessive. When the germ-cells of the hybrid are formed the seven pairs of chromosomes are reduced to seven singles. Since this reduction is a random one the hybrid produces eight kinds of pollen-cells and eight kinds of egg-cells, so far as these three characters are concerned. Consequently when the hybrid is selfed, in accordance with the Second Law of Mendel, we get on the average once in 64 times, a Dwarf Perpetual-flowering Full-double White Rose with the mixed characters of *multiflora* and *chinensis*.

Such was the origin of the Polyantha Pompon Rose "Paquerette," raised by M. Guillot in 1873, which introduced a new race of Roses to our gardens. (Fig. 1b.)

The chromosomes in Roses, as in other plants and animals, are relatively constant in size, shape and number for any particular individual. In the five genera of the Rose tribe there are minor differences in size and shape of the chromosomes, but in *Rosa* proper all the chromosomes are relatively the same in size and shape, though they differ remarkably in number. Six different types have been found with 14, 21, 28, 35, 42 and 56 chromosomes respectively in the body-cells. The interesting and important point is that all these numbers are multiples of seven. In the formation of the germ-cells and at certain other times the chromosomes may be seen working in sets of seven, or septets, as we call them. To cut a long story short, our genetical experiments at Cambridge have demonstrated that in *Rosa* proper there are five distinct septets or sets of seven chromosomes, which we distinguish as A, B, C, D, and E septets. Each septet of chromosomes carries a different set of genes, representing at least 100 specific, sub-specific and varietal characters. From this it follows that there are five fundamental species in the genus *Rosa* of Linnaeus, and that all the other species of this genus consist of various combinations of the chromosomes and characters of these five fundamental species. The five fundamental species are called diploids, because they contain two septets of chromosomes in their body cells; other Roses are called polyploids because they contain more than two septets. Triploids contain three septets, tetraploids four, pentaploids five, hexaploids six, and octoploids eight septets of chromosomes in their body-cells.

The first fundamental septet species which carries a pair of A septets of chromosomes is *Rosa sempervirens* (the oldest selected name) and its sub-species include *arvensis*, *moschata*, *phoenicea*, *abyssinica*, *Pissartii*, *Brunonii* (Fig. 8b and Pl. 1b), *Leschenaultiana*, *longicuspis* with its variety *lucens* (Pl. 1a), *gigantea* with its offspring *odorata* (the Tea Rose), *Soulieana*, *Helena*, *Rubus*, *Gentiana*, *laevigata* (with its offspring *sinica* *Anemone*), *Banksiae*, *microcarpa*, *chinensis* (with its offspring the Pink and Crimson Chinas), *anemoneflora*, *cathayensis* (with its offspring Crimson Rambler), *multiflora*, *Wichuraiana* (Fig. 7a), *Luciae*

Watsoniana, ~~*rubrifolia*~~, *setigera* and several new sub-species from China found at Kew and Cambridge in Mr. Cory's seedlings.

The AA septet species is distinguished by its climbing stems, sinuous recurved branches, stout dilated hooked to inclined prickles, uniformly narrow stipules with reflexed margins, petioles with stout curved pricklets, compound flowers placed on erect branchlets, narrow bracts, reflexed and deciduous sepals, petals with musk-Rose fragrance, disc broad and fleshy with contracted orifice, elongated exserted and thread-like styles arranged in a column, late-ripening fruits with 3-4 tiered achenes. The sub-species differ from one another in major alternative characters, but as a whole intergrade and are linked up with one another. These also differ from one another in their habitats and range of distribution, and have many Mendelian varieties. In some cases the sub-species overlap, but usually they occupy distinct geographical areas.



FIG. 2 (a).

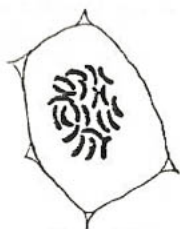


FIG. 2 (b).

Triploid Roses with 21 chromosomes in body-cells, 14 in female germ-cells and seven in male germ-cells.

- (a) Twenty-one chromosomes in body-cell of the old Crimson China Rose (AAA). This variety is still cultivated in China. (See page 46.)
- (b) Twenty-one chromosomes in body-cell of a French Cabbage Rose (AAC). In this variety a C septet of chromosomes has been lost from the old Cabbage Rose (AACC), causing a predominance of the A septet characters. (See page 49.)

The AA species is spread over the temperate and tropical regions of the Northern hemisphere from Western Europe, North Africa and Asia to the Western and Eastern States of North America in sunny and sheltered situations.

The second fundamental septet species which carries a pair of B septets of chromosomes is *Rosa sericea* (the oldest name), and its sub-species include *cabulica* (usually mislabelled *Beggeriana* in gardens), *Ecae*, *Webbiana*, *omeiensis*, *sertata* (Fig. 7c), *Willmottiae*, *Hugonis* (Pl. IIa), *xanthina* (of American gardens, not the one in British gardens which is a tetraploid *ochroleuca* with B and D septets), *gymnocarpa* and a new sub-species found at Cambridge. The BB septet species is distinguished by its rigid inclined stems, rigid shortnoded right-angled branches, stiletiform or compressed winged prickles, leaves crowded in axillary tufts, stipules narrowed to base, leaflets small to minute, base and apex rounded with broad apical teeth, flowers solitary (or rarely 1-4) wreathed on short lateral branches, bracts absent or rare, sepals erect and convergent in fruit, disc narrow and thin, petals with fruity or foetid scent, styles loose and contorted, fruits early-ripening and deciduous.

The BB species is distributed usually in exposed dry places from West to East in Asia and Western North America, none having been found in Europe, Africa or Eastern North America.

The third fundamental septet species which carries a pair of C septets of chromosomes is *Rosa rugosa* (the oldest name) and its sub-species include *coruscans*, *nipponensis* (Pl. IIb) (not *acicularis nipponensis* of gardens which is a tetraploid), *nitida* and two new sub-species found at Kew and Albury.

The CC septet species is distinguished by its thickset glandular bristly stems, spreading tortuous glandular bristly branches, prickles skewer-shaped to glandular bristles very unequal, leaves terminal crowded on surface of bush and early deciduous, stipules broad and clasping, flowers terminal on surface of bush, bracts oval to orbicular and clasping, sepals crown-like in fruit, petals with Old Rose fragrance, disc narrow and thick, styles crowded in curved sheaf, fruits with achenes two to three tiered placed on central cone and around the inner walls.

The CC species in its distribution is confined to the cold and foggy sea coasts of North Eastern Asia and North Eastern North America, none having been found in Europe, Africa, Western Asia or Western North America.

The fourth fundamental septet species which carries a pair of D septets of chromosomes is *Rosa carolina* (the oldest name) (of Linnaeus 1753, not his species of 1762 which is in part a tetraploid with A and D septets) and its sub-species include *cinnamomea* (Fig. 9a) of Linnaeus 1759 (not his species of 1753, which is a tetraploid with D and E septets) *davurica*, *Marettii*, *pisocarpa*, *Woodsii* *Fendleri*, *foliolosa*, *blanda* (Pl. IVa) and several new sub-species raised from seeds collected in North America.

The DD septet species is distinguished by its running erect slender stems, twiggy acute-angled branches, slender curved awl-shaped to straight needle-like prickles, terminally tufted leaves, flat to inrolled stipules (lower narrow and upper dilated), margins of leaflets undulate, upper teeth deep, flowers in close clusters scattered in axillary or terminal tufts, bracts concave oval crowded and leafy, sepals thin with deciduous tips, petals with spicy fragrance, disc obscure with wide orifice, styles short and straight, fruits rapid-ripening walls thin with hollow upper chamber.

This species is widely distributed in a more or less continuous area in cold and wet places in the North temperate regions of the northern hemisphere. It is more numerous in North America, where the sub-species overlap and produce natural crosses freely.

The fifth fundamental septet species is *Rosa macrophylla* (the oldest name) (Fig. 8a, Pl. IVb) and its sub-species include *corymbulosa*, *Giraldii*, *elegantula*, *persetosa* and two new sub-species from China found at Kew.

The EE septet species is distinguished by its straight and cany stems, drooping and sub-heliotropic branchlets, dagger-shaped ascending prickles, serpentine leaves with early deciduous leaflets, stipules with swollen base and dilated tips, leaflets with prominent and sub-parallel veins beneath, flowers heliotropic on drooping branchlets, bracts lance-shaped to egg-shaped long pointed, sepals erect and connivent in fruit with convex fleshy base forming the rim of the fruit, petals with faint fragrance, disc broad and thin concave in fruit, styles elongated included erect and stout, fruits elongated with neck and rim.

This species is apparently confined in its distribution to the Himalaya and Central China, and is usually found in wet and warm places. It is hardy in sheltered gardens in England, and there is a fine old specimen in the Botanic Garden at Cambridge.

POLYPLOID ROSES.

The other species of *Rosa* are polyploids with more than two septets of chromosomes, and these are all made up of various combinations of the chromosomes and characters of the five fundamental diploid species. Two distinct kinds of polyploids have been found in Roses.

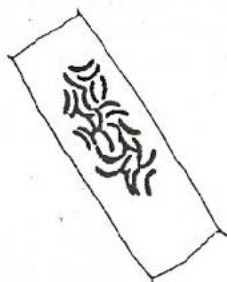


FIG. 3 (a).

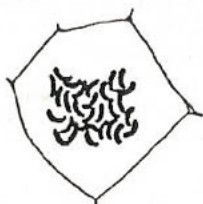


FIG. 3 (b).

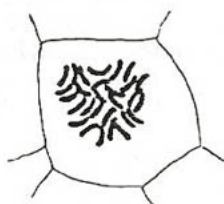


FIG. 3 (c).

Regular Tetraploid Roses with 28 chromosomes in body-cells and 14 in male and female germ-cells.

- (a) Twenty-eight chromosomes in body-cell of the old Cabbage Rose (AACC).
- (b) Twenty-eight chromosomes in body-cell of the Pompon Burgoyne Rose (AACC).
- (c) Twenty-eight chromosomes in body-cell of the Pompon Moss Rose (AACC).

(See page 49.)

(1) **Polyploid varieties** of diploid species in which the septets of chromosomes have been reduplicated. These polyploid varieties have one or two septets of chromosomes more than the diploid species to which they belong, but their specific characters are identical, showing that their original chromosome complement has been reduplicated. For example: Polyploid varieties of the AA diploid species have AAA (triploid) or AAAA (tetraploid) septets of chromosomes.

(2) **Polypld Species** in which the septets of chromosomes are differential. These are distinct species, differing from one another by one or more differential septets of chromosomes and characters. For example, the septets of chromosomes of one tetraploid species are AABB while those of another tetraploid species are CCDD, and so on through all the possible combinations of the five septets.

POLYPLOID VARIETIES.

So far 21 polypld varieties have been found in Roses, five tetraploids and 16 triploids. It is remarkable that all these are cultivated forms that have arisen in gardens. None has yet been found in a wild state. The old garden Rose Gloire de Dijon is a tetraploid variety of the Tea Rose with AAAA septets of chromosomes, and other tetraploid varieties are Mme. Alfred Carrière and Red Letter Day. A giant form of *cinnamomea* which I found in the garden of the late Canon Carew-Hunt at Albury, nr. Oxford, is a tetraploid variety of the diploid species *Rosa carolina* sub-species *cinnamomea* (DD) (Fig. 9a) with DDDD septets of chromosomes. A giant form of *Rosa macrophylla* was found in a garden at Khiva, and is known as var. *Korolkowii* (Pl. V, a & b). This is a tetraploid variety of the diploid species *Rosa macrophylla* (EE) (Fig. 8a & Pl. IVb), and has EEEE septets of chromosomes. There is a plant of this at Kew and another at Cambridge from Albury, and my material has been obtained from both of these plants.

From the horticultural point of view, this form with large flowers, fruits and leaves is a great advance and although the plant is a giant form in the size of its parts, it is no taller than the ordinary diploid species.

The 16 triploid varieties of Roses so far found all belong to the AA diploid species.

Eleven of these are forms of the old Crimson China Rose (*semperflorens*) whose seedling descendants have apparently remained triploid with AAA septets of chromosomes, since its introduction from China in 1791 (Fig. 2a). The original form figured by Curtis in the Botanical Magazine of 1794 is identical with some of the triploid forms of the Crimson China found in gardens to-day. Judging by Wilson's specimen

No. 3611, collected in a garden in Western Hu-peh these triploid varieties are still cultivated in China.

In the course of my researches I have found a curious case in this triploid (AAA) in which a whole septet of chromosomes has been thrown out of the nucleus of a body-cell, leaving it diploid (AA).

Among my material from La Belle Roseraie de L'Hay, Paris, there is a climbing China Rose with single red flowers which closely resembles the wild specimens of *chinensis* collected by Prof. Henry in Western Hu-peh (No. 1151) in his expedition of 1885-1888. On examination I found that this is a diploid form (AA) with fourteen chromosomes in the body-cells and seven in the male and female germ-cells. Twelve garden forms of *chinensis* examined prove to be diploids (AA), including the original plant of the Old Pink China introduced from China about 1789 (Fig. 1a) and the Green China Rose (Fig. 7b).

Of the remaining five triploid Roses (AAA), four belong to *chinensis* and one (Lady Hillingdon) to the Tea Roses (*odorata*). The original Pink Tea Rose (*odorata*) with double flowers introduced from China in 1809, and its yellow variety introduced in 1826, are still cultivated in Western Yunnan, China. Four forms, immediate descendants of these, have been examined and prove to be diploids (AA) with 14 chromosomes in the body-cells and seven in the male and female germ-cells. An analysis of their characters leads one to presume that the garden Tea Roses (*odorata*) were originally derived from crossings of Dwarf Double Perpetual flowering forms of *chinensis* with *gigantea*, both of which grow in Yunnan. Mendelian segregations in later generations of this cross would be expected to give the various forms and colours found in the Tea Roses. In such Roses as Jaune Desprez, Gloire de Dijon, Maréchal Niel and Niphetos it is easy to trace the characters of the ancestor *gigantea* and its yellow form *macrocarpa*. In view of this, it would be well worth while for Rose breeders to repeat these crosses with *gigantea*, using the more highly developed modern Roses. Some of these first crosses have recently been raised on the Continent and elsewhere, but it is important to realise that the first crosses will be Summer-flowering like *gigantea*, and that Mendelian segregation will not be evident until the second generation of breeding, when the true Perpetual-flowering will appear along with many other happy recombinations of form, texture, colour, fragrance and habit of growth.

POLYPLOID SPECIES.

So far all the wild polyploid Roses examined are polyploid species or hybrids with differential septets of chromosomes made up of various combinations of the chromosomes and characters of the A, B, C, D, and E septets. At least two distinct types of polyploid species may be recognised:—

- (1) Regular polyploid species with paired chromosomes.
- (2) Irregular polyploid species with both paired and single chromosomes.



FIG. 4 (a).



FIG. 4 (b).

Irregular Tetraploid Roses with 28 chromosomes in body-cells, 21 in female germ-cells and seven in male germ-cells.

- (a) Twenty-eight chromosomes in body-cell of *R. pomifera* (CDEE).
- (b) Twenty-eight chromosomes in body-cell of *R. rubrifolia* (ADDE).

(See page 58.)

REGULAR POLYPLOID SPECIES.

Since there are five differential septets A, B, C, D, and E, 26 regular polyploid species are possible, namely 10 tetraploids, 10 hexaploids, five octoploids and one decaploid. Of these 18 have so far been identified, namely nine tetraploids, seven hexaploids and two octoploids. These regular polyploid species are distributed in the Arctic and temperate regions of the Northern hemisphere and the most polyploid species (octoploid) are circumpolar so far as critically known.

REGULAR TETRAPLOID SPECIES.

Regular Tetraploid species with four septets are :—

Rosa Huntii, a new species from China, with a pair of A and a pair of B septets. This AABB species with 28 chromosomes in its body-cells and 14 in its male and female germ-cells was received by the late Canon Carew-Hunt from a missionary in China, but its precise habitat is unfortunately unknown. The plant, now in the Cambridge collection, well combines the characters peculiar to the A and B septets of chromosomes.

Its small flowers and fruits and sub-fœtid scent are not very attractive as a garden plant, but its large stout wing-shaped prickles and tall habit of growth make it a striking figure in the landscape, especially in winter time.

Rosa centifolia, the oldest Rose in cultivation, with a pair of A and a pair of C septets (Fig. 3a), has numerous sub-species, including *damascena*, *gallica*, *provincialis*, *pumila*, *parvifolia* and *Pomponia* (Rose de Meaux).

Sixty varieties of the type and its sub-species have been examined, including a number of garden Roses with double or semi-double flowers belonging to the Hybrid Perpetual, Gallica, Pompon (Figs. 3b & c), Cabbage and Moss Rose types. All are tetraploids (except one of the French Cabbage Roses, which is a triploid) with four septets of chromosomes (AACC) in the body-cells and two septets (AC) in the male and female germ-cells. All combine the characters peculiar to the A and C septets in various ways causing much variation. Genetic experiments show that the gene for mossing or compound glands in the Old Pink Moss Rose is a Mendelian dominant located in one of the chromosomes, but not in the other of the pair. The triploid French Cabbage Rose has in some way lost one of its C septets of chromosomes, leaving it AAC (Fig. 2b). The typical form of the tetraploid species (AACC) was already in cultivation at the time of Theophrastus, about 350 B.C., and was known to him by the same name, *Rosa centifolia*; it is still cultivated for its petals, which are made into Rose Water in France, Bulgaria, Persia and India.

Rosa palustris, with a pair of A and a pair of D septets with its sub-species *corymbosa*, *Hudsoniana*, *humilis grandiflora* (of gardens) and in part *carolina* of Linnaeus 1762 (not 1753).

Rosa Davidii (Pl. VII a, b & c) with a pair of A and a pair of E septets and its sub-species *setipoda*, *roseo-Moyesii*, *Fargesii*, and *crasse-aculeata*.

The AAEE species is represented by some interesting forms recently introduced from Central China, all of which are worth planting in the Wild Rose garden. The type is distinguished by its graceful habit, handsome foliage, and clusters of drooping fruits.

Rosa spinosissima (Pl. VIIa) with a pair of B and a pair of C septets and its sub-species *scotica*, *myriacantha*, *Ripartii* and *hispida* of Sims (not some *hispida* of gardens, which are hybrids).

The BBCC species has been represented in gardens for upwards of a century by the white, yellow and pink Scotch Roses.

Unfortunately its botanical history has been confused since the time of Linnaeus with the following species, which is BBDD.

Rosa pimpinellifolia, with a pair of B and a pair of D septets and its sub-species *hemispherica*, *lutea*, *lutescens*, *Verborgei* (Fig. 9b), *ochroleuca* (Pl. IX, a & b), *altaica* with its var., *grandiflora* (Pl. VIII, b & c), and *Rapini*.

The species BBDD includes a number of old cultivated Roses, including that well known bud-sport of *lutea* called "Austrian Copper," with its petals of two colours (red above and yellow beneath) a predecessor of the modern bicolor Rose Queen Alexandra. The BBDD species has a wide distribution from Wales to the Caucasus, Mongolia and Northern China.

It has been much confused by travellers and collectors with the former species BBCC, but those who have seen the BBCC species *spinosissima*, growing wild on the sand dunes of the coasts of England and France, and the BBDD species, *pimpinellifolia*, growing on the Jura Mountains in Switzerland, will at once appreciate the distinctness

of these two species. The habits of growth, habitats and distributions of these are fundamentally different, though since both species have 14 BB chromosomes in common about one-half of their characters are identical.

Rosa multibracteata, with a pair of B and a pair of E septets and its sub-species *reducta* and *bella*.

Rosa virginiana (= *lucida*), with a pair of C and a pair of D septets and its sub-species *baltica*, *suffulta*, *Lunellii* and *saturata*.

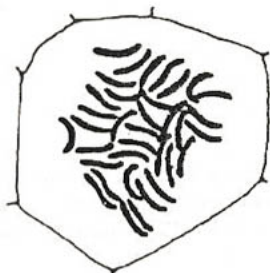


FIG. 5.

The pentaploid species *R. Froebelii* (ACDEE) from Kurdistan with 35 chromosomes in a body-cell (seven in the male germ-cells and 28 in the female germ-cells). This species is known in nurseries as *R. laxa*, though it is not the *R. laxa* of Retzius, which is a tetraploid DDEE, or of Lindley, which is a diploid DD.

(See pages 57 and 58.)

The CCDD species is represented by the *R. lucida* (Fig. 8c) of gardens, and is widely distributed in North America. The form *baltica* is apparently naturalised in Western Europe on the German shores of the Baltic, and at the mouths of the Elbe and the Loire.

Rosa pendulina (= *alpina*) (Pl. VI, a & b), with a pair of D and a pair of E septets, and its sub-species *pyrenaica*, *laxa* of Retzius (not of Lindley nor the garden *laxa*, which is a pentaploid), *oxyodon*, *lagenaria* and *intercalaris*.

The DDEE species has a wide distribution in the Alpine regions of Europe, from the Pyrenees to the Carpathians. In Asia it extends to

the Caucasus, Turkestan and Mongolia. I have not yet been able to identify it positively in either China or North America, though I suspect that Tackholm's tetraploid forms of *R. blanda* belong here. I have studied this species closely in five cantons of Switzerland, and have collected at least 20 distinct varieties there. I found that this species grows in a peculiar habitat, and only at altitudes between about 3,000 and 6,000 feet above sea-level. In gardens early in the nineteenth century this species was often confused with *cinnamomea*. (Cf. The Boursault Rose (AD)).

REGULAR HEXAPLOID SPECIES.

Regular Hexaploid species with six septets are comparatively rare, only 33 being found out of 1,006 examined.

Rosa Wilsonii, with a pair of A, B and C septets.

The AABBC species is a native of North Wales, North Ireland and Scotland, and we owe its determination as a regular hexaploid to the researches of Dr. Kathleen Blackburn and Dr. Heslop Harrison.

These authors give good reasons in support of the theory that this species arose as a natural hybrid between *R. spinosissima* ♀ (BBCC) and *R. tomentosa* ♂ (AACDE). The female germ-cells would carry in this case BC septets, while the male germ-cells would carry the A septet only, as we know from experiments. The resulting hybrid would be a triploid ABC, which by a duplication of its chromosomes, known to occur in many cases, would produce the regular hexaploid species, AABECC. In this way a new species would arise by hybridisation. This creation of new species may be going on at the present time, though it seems strange that so far no triploid forms have been found in a wild state.

Rosa manca, with a pair of A, B and D septets, a species from the Rocky Mountains of North America.

Rosa Moyesii, with a pair of A, B and E septets.

The AABBE species is well known in gardens, with its large, persistent and conspicuous dusky red flowers and its long handsome scarlet-red fruits and graceful foliage (Figs. 6a, 9c, Pl. XI, a & b). It is a native of Central China, and as a mother plant does not hybridise at all freely with other species.



FIG. 6 (a).

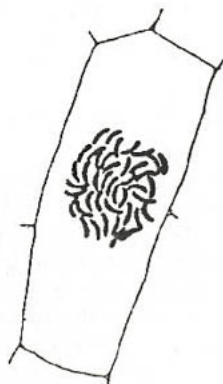


FIG. 6 (b).

Hexaploid Roses with 42 chromosomes in body-cells.

- (a) The regular hexaploid Rose *R. Moyesii* (AABBE) with 42 chromosomes in body-cell (21 in male and female germ-cells).
- (b) The irregular natural hybrid hexaploid Rose $\times$ *R. alba* (AACCDE) with 42 chromosomes in body-cell (23 in female germ-cells and 14 in male germ-cells).

(See also pages 61 and 62.)

Rosa nutkana (Pl. X, a & b, Fig. 8d), with a pair of A, D and E septets.

The AADDEE species is a native of Western North America. It is chiefly distinguished by its hard crimson fruits, which persist long after the leaves fall and are at their best in this country about Christmas time. As a mother parent, this species hybridises with other species such as *R. Moyesii* (AABBE) *R. Davidii* (AAEE) and its sub-species *setipoda* (AAEE) with extraordinary freedom.

Large numbers of these hybrids have been raised at Burbage and grown on at Cambridge; they seem to be very fertile, and the F_2 generation is awaited with much interest, since so many Rose hybrids are sterile.

Rosa Bourgeauiana, with a pair of B, C and D septets.

Rosa Engelmannii, with a pair of B, D and E septets.

Rosa Sayi, with a pair of C, D and E septets.

The three hexaploid species above *R. Bourgeauiana* (BBCCDD), *R. Engelmannii* (BBDDEE) and *R. Sayi* (CCDDEE) have by most authors been included in the octoploid species *R. acicularis* (BBCCDDEE). In view of the presence of similar septets of chromosomes and characters in these species it is easy to see how the confusion has arisen. From the material sent to me by Professor Cockerell and Dr. Eileen Erlanson it is evident that these hexaploid species grow round Lake Baikal in Siberia as well as in Canada and Michigan.

OCTOPLD SPECIES.

Regular octoploid species with eight septets are even more rare, only eight being found out of 1,006 Roses examined.

Rosa Tackholmii, a new species with a pair of A, B, C and D septets, apparently from Iceland (*cf. R. hibernica* Hooker).

Rosa acicularis, with a pair of B, C, D and E septets. This is a circumpolar species, the precise distribution of which has not yet been critically worked out owing to its confusion with the three hexaploid species above.

IRREGULAR POLYPLOID SPECIES.

The irregular polyploid species with both paired and single septets of chromosomes are of peculiar interest and present some remarkable features. They are confined in their distribution to the Old World in

temperate Europe and Western Asia, covering an area more or less conterminous with that of the Pleistocene Ice sheet at its maximum southern and eastern limits of influence.

These species differ from one another by one or more septets of chromosomes. Out of 180 different combinations of the five septets possible only 25 have so far been identified, and six of these are evidently natural hybrids growing near their putative parents. Three of the septet combinations have been made genetically, thus demonstrating experimentally the possible hybrid origin of these irregular polyploid species.

So far as these species have been tested genetically (12 in my experiments), all appear to be facultatively apomictical. That is to say as a rule they produce, from apparently normal seeds, plants which strictly resemble in all their characters the mother parent, just as if they had been grown from cuttings. These seedlings also have the same number and distribution of chromosomes as the mother parent. My researches into the nature of this phenomenon are not yet completed, but so far the evidence suggests that it is due either to the non-reduction of the chromosomes in the egg-cell and embryo-sacs are formed with the same number of chromosomes as are present in the body-cells without fertilisation or it may be due to homozygous self-fertilisation, the paired A septet, which alone is functional in the male germ-cells of *R. canina* (AABDE), being homozygous or pure-breeding in its genes through a previous duplication of the A septet of chromosomes. The single septets B, D and E functional in the female germ-cells are of necessity homozygous or pure breeding being composed of single chromosomes. Whatever may be the explanation of this curious phenomenon of apomixis, the fact itself is of considerable practical importance to the Rose grower. Armed with this knowledge the grower can now with sufficient certainty for practical purposes proceed to select any type of Briar Stock that he may consider suitable for budding his Roses, save the seeds produced thereon, all of which will produce seedlings identical with the mother plant. That this important fact has previously escaped observation is due to the random collection of Briar Seeds from a crowd of variable individuals giving a corresponding variable result, whereas a selection of seeds from individual

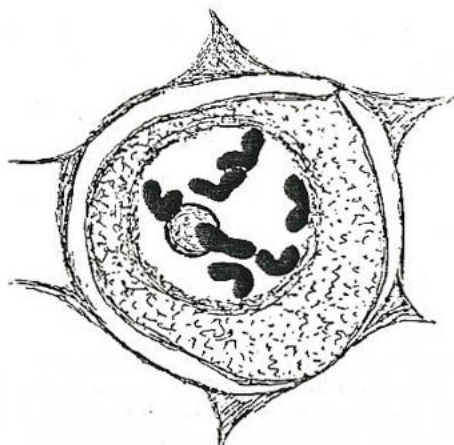


FIG. 7 (a).



FIG. 7 (b).



FIG. 7 (c).

Early germ-cells of diploid Roses with seven pairs of chromosomes preparing to reduce in order to form pollen-grains each with seven single chromosomes.

- (a) *R. sempervirens*, sub-sp. *Wichuriana* (AA), from Japan. (See page 41.)
- (b) The Green China Rose (AA) (in this case the pollen aborts although the first stages of formation are carried through). (See page 47.)
- (c) *R. sericea*, sub-sp. *sertata* (BB), from China. (See page 43.)

plants will, as a rule, give a pure line of true breeders. Thus seedling Briars will be as true to type as Cutting Briars. The fact that this apomixis in Roses is facultative means that occasionally foreign pollen is introduced and variable crosses arise. Our genetic experiments show that in the *Caninae* almost any crosses can be obtained, and we know that the female germ-cells partially reduce and prepare themselves for fertilisation, though in an unique way.

These occasional crosses will, however, be of little moment to the practical grower, as in most cases the incidence of outcrossing is slight. For instance, in my experiments with *R. Froebelii* (Fig. 5) = (*laxa* hort.) out of more than 100,000 seedlings raised from open flowers in an acre of mixed Briars only three seedlings were crosses; all the rest were pure *Froebelii*, identical with the mother plant.

Another peculiarity presented by the irregular polyploid species which at present is unique in plants and animals is the phenomenon of a *regular but unequal* reduction division in the female germ-cells, which causes them to produce final female germ-cells (gametes) carrying from two to five times as many septets of chromosomes as their male germ-cells.

For example the ordinary Briar *R. canina* (AABDE) has four septets of chromosomes (ABDE) in the female germ-cells and only one septet (A) in the male germ-cells. Consequently reciprocal crosses with *R. canina* are entirely different in their chromosome content and, therefore, in their characters.

Thus *R. rugosa* (CC) ♀ crossed with *R. canina* (AABDE) ♂ gives the diploid cross AC with no trace of the B, D and E septet characters, while the reverse cross *canina* ♀ × *rugosa* ♂ gives quite a different cross ABCDE, which bears all the five septet chromosomes and characters. All the irregular polyploid species are fully fertile in spite of their pollen being irregular and only partly fertile. They produce apomictical or sexual seeds in abundance, and maintain themselves so well in ordinary and even unfavourable conditions that they largely dominate the Rose population in Europe. For instance, all the species

of the Section *Caninae* (in a broad sense), commonly known as Briars, belong to the irregular polyploid species, and are either tetraploid, pentaploid or hexaploid.

IRREGULAR TETRAPLOID SPECIES.

Irregular Tetraploid species with paired and single septets are :—

Rosa omissa, with a paired A and single C and D septets.

Rosa recondita, with a paired C and single D and E septets.

Rosa mollis, with a paired D and single C and E septets.

Rosa pomifera, with a paired E and single C and D septets (Fig. 4a).

Rosa rubrifolia, with a paired D and single A and E septets (Fig. 4b).

The three species with C, D and E septets are all true *Villosae*.

PENTAPLOID SPECIES.

Pentaploid species with paired and single septets are :—

Rosa agrestis, with a paired A and single B, C and D septets.

Rosa canina, with a paired A and single B, D and E septets.

Rosa micrantha, with a paired A and single B, C and E septets.

Rosa tomentosa, with a paired A and single C, D and E septets.

Rosa rubiginosa, with a paired B and single A, C and D septets.

Rosa elliptica, with a paired B and single A, C and E septets.

Rosa glutinosa, with a paired C and single B, D and E septets.

Rosa pseudo-mollis, with a paired D and single A, B and C septets. (Found on Limepit Hill, near Cambridge, and is probably a natural hybrid from *rubiginosa* ♀ and *mollis* ♂, which grow with it.)

Rosa coriifolia, with a paired D and single A, C and E septets.

Rosa glauca, with a paired D and single A, B and E septets.

Rosa Froebelii, with a paired E and single A, C and D septets (= *laxa* hort.) (Fig. 5).

IRREGULAR HEXAPLOID SPECIES.

Irregular hexaploid species with paired and single septets are :—

Rosa Pouzinii, with a paired A and single B, C, D and E septets.

Rosa inodora, with a paired B and single A, C, D and E septets.

Rosa Jundzillii, with a paired C and single A, B, D and E septets.

EXPERIMENTAL DETERMINATION OF SPECIES.

The *experimental proof* of these analyses rests entirely on genetical experiments, many of which have been already carried out. Space will not allow these to be presented here, but in the Summer of 1927 I was able to demonstrate these experiments to the Genetical Society when they met at Cambridge.

From the scientific point of view these experiments with Roses have thrown a good deal of light on the problem of species. The old and much vexed question—what is a species?—is now, so far as the Rose is concerned, no longer a question of the personal opinion of doctors who differ; it is simply a matter of genetical experiments combined with the counting of the chromosomes in critical cases, while in ordinary cases the species can be determined by the use of a taxonomic table of the septet characters of the five fundamental species.

The point of real importance is that with modern methods of analysis we now have experimental proof that *a species is a real entity* made up of certain chromosome sets with their complexes of associated genes. The old systematists instinctively recognised this, though in their day they were unable to demonstrate it experimentally.

By the same methods we are also able to determine definitely the sub-species within the species, and the varieties within the sub-species. This clears the way for a better understanding of the distribution of Roses in space and time, and in the end will no doubt help to solve the problems of the evolution and the origin of the species.

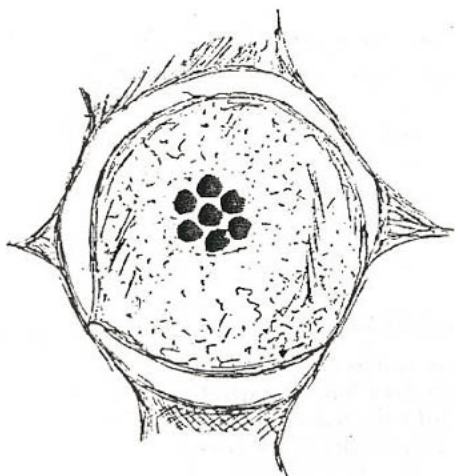


FIG. 8 (a).

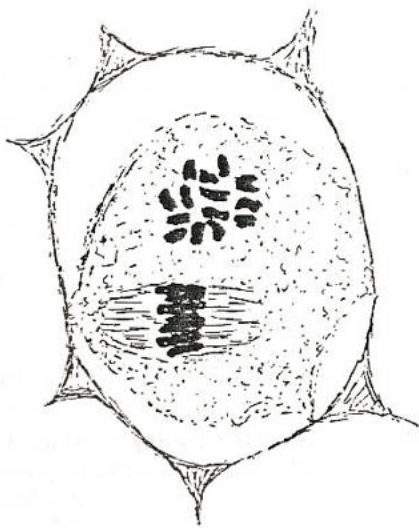


FIG. 8 (c).

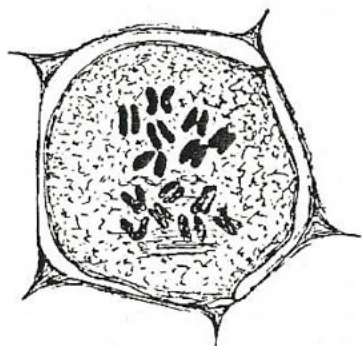


FIG. 8 (b).

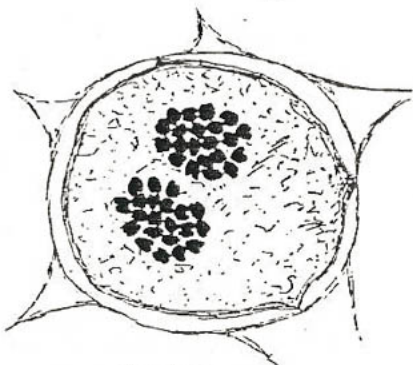


FIG. 8 (d).

Later stages of pollen formation. The formation of four pollen grains from a germ-cell, each of which will contain one-half of the number of chromosomes present in the body-cells.

- (a) *R. macrophylla* (EE diploid) with seven pairs of chromosomes about to reduce. (See page 44.)
- (b) *R. sempervirens*, sub-sp. *Brunonii* (AA diploid) final division of the chromosomes in the cell to form four pollen grains each with seven chromosomes. (See page 41.)
- (c) *R. virginiana*, sub-sp. *lucida* (CCDD tetraploid), the 14 pairs of chromosomes reduced and now preparing to divide to form four pollen grains each with 14 chromosomes. (See page 51.)
- (d) *R. nutkana*, sub-sp. *Nuttalliana* (AADDEE hexaploid), the 21 pairs of chromosomes reduced and dividing to form four pollen-grains each with 21 chromosomes. (See page 53.)

IMPROVEMENT OF GARDEN ROSES.

We now come to consider how we can apply these new scientific facts to the improvement of our garden Roses. Perhaps the best way to do this will be to go through our garden Roses and see what they really are in their septet characters. The oldest cultivated Roses, *centifolia*, *gallica* and *damascena*, cultivated by the Greeks, Romans and Egyptians are tetraploids with paired A and C septets. The old Chinas and Tea Roses cultivated in China for centuries are diploids with paired A septets, or triploid and tetraploid varieties with three or four A septets. The old Noisettes and the new Polyantha Pompon Roses are diploid with a pair of A septets. The Boursault Rose is a diploid hybrid with single A and D septets. The old Bourbon is a triploid hybrid with a paired A septet and a single C septet. The old Hybrid Perpetuals are, for the most part, tetraploids with paired A and C septets. The old Hybrid Teas are tetraploids with three A septets and one C septet, while some of the modern H.T.'s are tetraploids with four A septets. The original *Pernetiana* seedling was a tetraploid with single septets of A, B, C and D, while some later varieties have three septets of A and one B septet. The old natural hybrid $\times$ *Rosa alba* (Fig. 6b) and its offspring, Maiden's Blush, is a hexaploid with paired A and C septets and single D and E septets. Most of the Penzance Hybrid Sweet Briars are hexaploids with paired A and C septets and single B and D septets, though Lady Penzance has paired B and D septets and single A and C septets, while Catherine Seyton is a pentaploid with a paired B septet and three single A, C and D septets. From these analyses it is evident that in order to break new ground in Roses it is necessary to introduce the chromosomes and characters of the E septet into our present A, B, C and D Roses. This can be done by crossing with such species as *Rosa Moyesii* (δ) (Fig. 6a, 9c, Pl. XI, a & b), a hexaploid from China with paired A, B and E septets, or *Rosa nutkana* (?) (Pl. X, a & b, Fig. 8d), a hexaploid from North America with paired A, D and E septets. A similar result can be obtained by crossing with *Rosa rubrifolia* (?) (Fig. 4b), a tetraploid from the Alps, with a paired D septet and single septets of A and E. To get the desired result, however, care must be taken to use this species as the female parent since the pollen cells only carry the single D septet, which gives the characters of *cinnamomea* only, while the egg-cells carry the three

septets A, D and E, which give the characters of *rubrifolia*. In the same way the hexaploid natural hybrid $\times$ *Rosa alba* (Fig. 6b) carries in its egg-cells the four septets A, C, D and E, while the pollen-cells carry only two septets, A and C. It is only by using *alba* as the female parent that one can get the *alba* characters; in using *alba* as the male parent one only gets the characters of *centifolia*. *R. Davidii* (Pl. VII, a, b & c) from China, a tetraploid with paired A and E septets, would provide an excellent parent for this purpose, as well as its sub-species *Fargesii* with large flowers and fruits, another sub-species *setipoda* with its graceful habit, leaves and bunches of flowers followed by drooping fruits. One drawback to the use of the last species is that while the flowers appear in large clusters, yet for the most part the fruits set singly.

Hybrids between garden Roses and the above species are more likely to be fertile than direct hybrids with the pure EE species, *Rosa macrophylla*, which would give, for the most part, sterile triploids. Fertility in the second generation is necessary in the formation of a new race of Roses, since it is only in the second generation that we can get the recombinations of characters that we require, and many of the desirable qualities in garden Roses are recessive in the first generation. We now know definitely that sexual fertility is largely bound up with the pairing of the chromosomes present in complete septets. The chief desirable characters carried by the E septet are smooth, erect, cany stems, graceful foliage, large brilliant flowers and long-necked, pendulous fruits of various colours. These characters would be a welcome addition to our garden Roses, and may be secured in the second generation of breeding, if the breeder has a bit of luck and follows it up. In attempting to add these new characters, however, great care must be taken not to lose the desirable characters of form, colour, fragrance and perpetual flowering that we already have, and here arises a real difficulty, which a knowledge of the septet characters will help us to surmount. For instance, the A septet provides us with the delicate translucent colours of the China and Tea Roses, while the combination of the A and C septets gives us the deep velvety crimson of the Hybrid Perpetual, as well as the brilliant scarlets. The B septet gives us the rich yellow of *lutea* which comes out in some of the *Pernetianae*. The C septet provides us with the delicate and refined Old Rose fragrance of the Cabbage Rose, the A septet gives us the

odour of the Musk and Tea Rose, while the combination of both A and C septets produces the rich damask perfume of some of the old Hybrid Perpetuals. The B septet gives us some disagreeable odours, the D septet provides some spicy scents, while the E septet gives little fragrance. True perpetual-flowering is peculiar to the A septet. It is unknown in a wild state, though I have observed two definite cases in wild seedlings from China raised at Cambridge. It first appeared as a recessive mutation in Chinese gardens in the sub-species *chinensis*. The gene for perpetual flowering is either identical or very closely linked in the same chromosome with the gene for dwarf habit of growth. This should assist the breeder materially in creating a dwarf perpetual *Moyesii*.

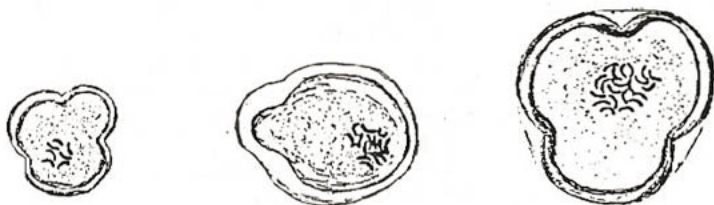


FIG. 9 (a).

FIG. 9 (b).

FIG. 9 (c).

Young pollen grains showing the reduced number of chromosomes.

- (a) The diploid *R. carolina*, sub-sp. *cinnamomea* (DD), with seven chromosomes in germ-cell (14 in body cells).
- (b) The tetraploid *R. pimpinellifolia*, sub-sp. *Verborgei* (BBDD), with 14 chromosomes in germ-cell (28 in body-cells).
- (c) The hexaploid *R. Moyesii* (AABBEE) with 21 chromosomes in germ-cell (42 in body-cells).

There are also further but much more remote possibilities of raising entirely new races of garden Roses by the use of four other distinct diploid species usually classed as *Rosa*, but which our septet analyses prove to be four distinct though related genera of the Rose tribe. One of these, *Hesperhodos minutifolia*, with its sub-species *stellata* and *mirifica*, so far refuses to cross with *Rosa*. This primitive genus from the Western United States is a desert plant with small leaflets resembling some of the fossil Roses found in the Miocene beds of Colorado, which are the oldest Roses known. It has large, striking

flowers and prickly fruits; in the distance the plant is not unlike a gooseberry bush. Two of the other genera have produced hybrids with *Rosa*, namely *Ernestella bracteata* from China and India, which, though rather tender, has large white woolly late autumnal flowers with bunched bracts; it has been crossed with a yellow Tea Rose, giving the lovely Mermaid which, though bearing single flowers, is quite sterile at Burbage and Cambridge.

Platyrhodon macrophylla, from China and Japan, the so-called Chestnut Rose with cup-shaped fruits covered with fleshy spines seems more promising in its fertility since I have succeeded in raising the second generation of a hybrid with *Rosa rugosa*. The results, however, though extremely interesting from the scientific point of view, are not very promising horticulturally, since the grandparent *rugosa* has been reproduced in facsimile several times, while the others resemble the parent hybrid with strange mutational variations.

The remaining genus, *Hulthemia persica*, from the salty deserts of Central Asia, is the Rose with simple leaves and no stipules, with Cistus-like flowers, yellow blotched with red; it has been crossed with *Ernestella*, with which it gave the beautiful hybrid known as *R. Hardii*, which, however, is quite sterile at Burbage and Cambridge, and is difficult to keep alive out-of-doors, though it luxuriates in a greenhouse. Since one of the parents comes from the hot plains of Bengal this is not altogether surprising. The other parent, *Hulthemia*, is equally difficult to cultivate in our wet climate, though it survives in Paris and the South of France.

In view of these facts there does not seem to be much hope of raising new races of garden Roses outside the genus *Rosa*, of Linnaeus. In that genus, however, there is plenty of scope by introducing, as suggested, the chromosomes and characters of the E septet, which are entirely lacking in our present garden races.